

University of Groningen

Towards a unified understanding of lateralized vision

Brederoo, Sanne G.; Van der Haegen, Lise; Brysbaert, Marc; Nieuwenstein, Mark R.; Cornelissen, Frans W.; Lorist, Monicque M.

Published in:
Cortex

DOI:
[10.1016/j.cortex.2020.08.029](https://doi.org/10.1016/j.cortex.2020.08.029)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2020

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Brederoo, S. G., Van der Haegen, L., Brysbaert, M., Nieuwenstein, M. R., Cornelissen, F. W., & Lorist, M. M. (2020). Towards a unified understanding of lateralized vision: A large-scale study investigating principles governing patterns of lateralization using a heterogeneous sample. *Cortex*, 133, 201-214. <https://doi.org/10.1016/j.cortex.2020.08.029>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



Research Report

Towards a unified understanding of lateralized vision: A large-scale study investigating principles governing patterns of lateralization using a heterogeneous sample



Sanne G. Brederoo^{a,b,c,*}, Lise Van der Haegen^d, Marc Brysbaert^d,
Mark R. Nieuwenstein^{a,b}, Frans W. Cornelissen^{b,c,e} and
Monique M. Lorist^{a,b,c}

^a Department of Experimental Psychology, Faculty of Behavioural and Social Sciences, University of Groningen, Groningen, the Netherlands

^b Research School Behavioural and Cognitive Neurosciences, University of Groningen, Groningen, the Netherlands

^c Cognitive Neuroscience Center, Department of Biomedical Sciences of Cells and Systems, University Medical Center Groningen, University of Groningen, Groningen, the Netherlands

^d Department of Experimental Psychology, Faculty of Psychology and Educational Sciences, Ghent University, Ghent, Belgium

^e Laboratory of Experimental Ophthalmology, University Medical Center Groningen, University of Groningen, Groningen, the Netherlands

ARTICLE INFO

Article history:

Received 23 August 2019

Reviewed 15 November 2019

Revised 14 April 2020

Accepted 31 August 2020

Action editor Gus Buchtel

Published online 29 September 2020

Keywords:

Lateralization

Face processing

Word processing

Language dominance

Handedness

ABSTRACT

While functional lateralization of the human brain has been a widely studied topic in the past decades, few studies to date have gone further than investigating lateralization of single, isolated processes. With the present study, we aimed to arrive at a more unified view by investigating lateralization patterns in face and word processing, and associated lower-level visual processing. We tested a large and heterogeneous participant group, and used a number of tasks that had been shown to produce replicable indices of lateralized processing of visual information of different types and complexity. Following Bayesian statistics, group-level analyses showed the expected right hemisphere (RH) lateralization for face, global form, low spatial frequency processing, and spatial attention, and left hemisphere (LH) lateralization for visual word and local feature processing. Compared to right-handed individuals, lateralization patterns of left-handed and especially those who are RH-dominant for language deviated from this 'typical' pattern. Our results support the notion that face and word processes come to be lateralized to homologue areas of the two hemispheres, under influence of the RH- and LH-specializations in global form, local feature, and low and high spatial frequency processing. As such, we present a more unified understanding of lateralized vision, providing evidence for the input asymmetry and

* Corresponding author. Department of Experimental Psychology, Grote Kruisstraat 2/1, 9712 TS, Groningen, the Netherlands.

E-mail addresses: sannebrederoo@gmail.com, s.g.brederoo@rug.nl (S.G. Brederoo).

<https://doi.org/10.1016/j.cortex.2020.08.029>

0010-9452/© 2020 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

causal complementarity principles of lateralized visual information processing. The absence of correlations between spatial attention and lateralization of the other processes supports the notion of their independent lateralization, conform the statistical complementarity principle.

© 2020 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Functional lateralization, or the differential specialization of the two cerebral hemispheres, enables the human brain to process a multitude of different types of information in an efficient and optimized manner (Hellige, 1993). At the population level, this division of labor is expressed in ‘typical’ patterns of lateralization, such as left-hemisphere (LH) dominance for most language-related processes, and right-hemisphere (RH) dominance for face processing (Behrmann & Plaut, 2015). At the same time, individuals can still differ in direction and strength of lateralization to such an extent that some people show RH-dominance for language, whereas others show no clear evidence for either hemisphere being dominant for language-related tasks (Mazoyer et al., 2014; Rasmussen & Milner, 1977). To understand the principles underlying the distribution of functions across the two hemispheres in both typical and reversed or atypical lateralization, the current study examined the relationships between hemispheric specializations for an array of processes including and subserving language and face perception, using a sample of participants that could be expected to show considerable heterogeneity in their direction and strength of lateralization based on variability in their handedness and/or known hemispheric dominance for language.

To date, only few studies have examined the relationships between different lateralized processes –often including measures of language and face processing, and the results of these studies have led to different views on the existence and nature of these relationships. Specifically, previous studies have suggested a number of hypotheses about the principles that may govern patterns of lateralization, which we here summarize as the *statistical complementarity* (Bryden, Hécaen, & DeAgostini, 1983), *causal complementarity* (Bryden et al., 1983), and *input asymmetry* (Andresen & Marsolek, 2005) principles. Each of these three principles assumes that various processes are lateralized, and attempt to explain patterns of lateralized processing.

According to the statistical complementarity principle, each process has a certain probability of being lateralized to one hemisphere, which is independent of the probability that other processes are lateralized to the same or the other hemisphere. Consequently, certain brain processes may show consistent lateralization to contralateral hemispheres at the population level, but there is no causal relation underlying this division of labor. In line with this view are the results of a factor-analytic study of cortical activity during rest, supporting the independence of lateralized brain systems involved in vision, internal thought, attention, and language (Liu, Stufflebeam, Sepulcre, Hedden, & Buckner, 2009). This claim

was further corroborated by a review by Badzakova-Trajkov, Corballis, & Häberling (2016), showing that most evidence supports independent lateralization of different processes, especially with regard to processes that operate on information from different domains. In support of the conclusions from their literature review, the authors additionally present the results of a factor-analysis on neuroimaging data, suggesting independently lateralized systems governing spatial attention, word generation, and face processing (Badzakova-Trajkov et al., 2016).

In contrast to the statistical complementarity principle, the causal complementarity and input asymmetry principles both assume that lateralization of one process does depend on lateralization of others, with the former accounting for *functional segregation* (i.e., lateralization of different functions to opposite hemispheres) and the latter for *co-lateralization* (of different functions to the same hemisphere) (Vingerhoets, 2019). According to the causal complementarity principle, once a certain process is lateralized to a specific cortical area in one hemisphere, there is limited room for specialization of other processes in this area (Andresen & Marsolek, 2005; Badzakova-Trajkov et al., 2016; Cai, Van der Haegen, & Brysbaert, 2013; Gerrits, Van der Haegen, Brysbaert, & Vingerhoets, 2019). As a consequence, other types of information that may initially have been processed by the now occupied area, will become lateralized to homologous areas in the contralateral hemisphere. Support for this notion has been provided by Dundas, Plaut, & Behrmann (2015). In their study, Dundas and colleagues presented word and face stimuli (both assumed to recruit the middle fusiform gyrus) to a group of 7–12 year-olds, who varied in their word recognition competence, while measuring the electro-encephalography (EEG) response. The results showed that the more LH-lateralized the children were for word processing, the more RH-lateralized they were for face processing, as reflected by the differing magnitudes of the measured event-related potentials (ERPs) in response to word and face stimuli. Aside from this evidence for causal complementarity between face and visual word processing, a number of studies have suggested causal complementarity for face processing and the production of language during speech. For example, Gerrits et al. (2019) showed a correlation between LH-lateralization of brain regions that were active during language production and RH-lateralization of brain regions that were active during face perception.

The question then arises why visual word processing becomes lateralized to the LH and face processing to the RH, rather than the other way around. Behrmann and Plaut (2013) suggest that in order to arrive at efficient word and face processing, there is pressure for intrahemispheric connectivity to

areas governing the representation of information necessary for such processing. While word and face processing demand similar resources (such as central vision, a possible reason they both engage the fusiform gyrus [Hasson, Levy, Behrmann, Hendler, & Malach, 2002]), they also differ in the types of information necessary from lower levels in the processing hierarchy. In the case of visual word and face processing, this difference would concern cortical areas devoted to language, which are necessary for processing of the former but not the latter type of visual information. Indeed, previous studies have shown a positive correlation between lateralization for language production (i.e., verbal fluency) and visual language perception (i.e., word reading) (Gerrits et al., 2019; Van der Haegen & Brysbaert, 2018). As such, hemispheric dominance for speech can be seen as a candidate for driving the direction of the complementary lateralization of word and face processing.

The input asymmetry principle captures this co-lateralization principle more generally, in proposing that lower-level processes subserving higher-level processes will drive ipsilateral lateralization of the latter (Andresen & Marsolek, 2005). This principle is, for example, reflected in a theory by Ivry and Robertson (1998), which has its basis in the assumption that the LH selectively processes relatively high frequency information, while the RH selectively processes relatively low frequency information. Any higher-level visual process that operates on a specific range of spatial frequencies, therefore, would also be lateralized to the hemisphere specialized for lower-level processing of that frequency range. As the holistic processing of a face has been shown to be affected by removing low spatial frequency (LSF) but not high spatial frequency (HSF) information (Goffaux & Rossion, 2006), the strength of RH-lateralization for face processing would thus be expected to depend on the strength of RH-lateralization for LSF processing. Conversely, word processing has been shown to rely on HSF information (Ossowski & Behrmann, 2015), and the strength of LH-lateralization would thus be expected to depend on the strength of LH-lateralization for HSF processing. This idea has been supported by findings of differential sensitivity to spatial frequency information in the LH and RH fusiform gyri (Woodhead, Wise, Sereno, & Leech, 2011). Specifically, they used sine-wave gratings to show that the LH fusiform gyrus—an area specialized in word processing—responds more strongly to the presentation of HSFs, while the RH fusiform gyrus,—specialized in face processing—, responds more strongly to the presentation of LSFs.

In summary, previous studies examining the relationships between different instances of hemispheric specialization have resulted in diverging claims about the existence and nature of these relationships. Specifically, the statistical complementarity principle assumes no relation between lateralization of different processes, while the other two principles do. The causal complementarity principle explains how different processes become functionally segregated to the two hemispheres. Furthermore, the input asymmetry principle proposes that cortical areas devoted to different processes within a processing hierarchy benefit from intrahemispheric connectivity and thus promote co-lateralization of these processes to the same hemisphere. As such, the causal complementarity and input

asymmetry account for two sides of the same coin: the former proposing contralateral specialization of processes recruiting similar resources (e.g., faces and words), the arrangement of which in turn is driven by ipsilateral specialization of processes within a processing hierarchy (e.g., faces and low spatial frequencies), as proposed by the latter. As such, the causal complementarity and input asymmetry principles are not mutually exclusive, while both are mutually exclusive with the statistical complementarity principle.

1.1. Present study

In the present study, we aim to shed light on these relationships by investigating the lateralized processing of different types of visual stimuli, using a large sample of participants ($n = 122$) who would be expected to show heterogeneity in both strength and direction of lateralization because of variation in, amongst other things, handedness. Specifically, we examined the relationships between behavioral indices of lateralized processing of visual words, faces, global and local elements, high and low spatial-frequency information, and the distribution of spatial attention, using tasks that we had previously found to produce replicable lateralization indices for population-typical lateralization in a sample of right-handed participants (see Brederoo, Nieuwenstein, Cornelissen, & Lorist, 2019). Using this series of tasks we aimed to test previous claims proposing causal complementarity between the processing of words and faces, and to determine whether any such complementarity might relate to hemispheric specialization for lower-level perceptual processes that rely on similar information (i.e., high spatial frequencies and local elements in the case of visual words vs low spatial frequencies and global form in the case of faces), as proposed by the input asymmetry principle. Furthermore, we will test whether lateralization of these several types of visual information is statistically independent from lateralization of spatial attention, which is often measured in the visual domain with the landmark task (e.g., Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Cai et al., 2013).

In examining the relationships between lateralized processes, we also aimed to determine whether certain processes are consistently mediated by the same or by different hemispheres, irrespective of which hemisphere this might be. That is, we investigated whether people who show population-typical lateralization for one process (e.g., LH-dominance for recognizing visual words) also show population-typical lateralization for another (e.g., LH-dominance for high spatial frequencies), and whether people with reversed lateralization for one process then also show reversed lateralization for the other processes. To be able to address this question, we included a number of participants (all left-handed) whom were known to show RH-dominance for language processing. Such RH-dominant individuals are difficult to find in random samples, which is why we recruited them from a sample of left-handed participants whose language dominance had previously been assessed using functional magnetic resonance imaging (fMRI) and behavioral methods in a study by Van der Haegen, Cai, Seurinck, & Brysbaert (2011). By including a sample of this rarely studied group of participants, our study offered a unique opportunity to determine if

Table 1 – Predictions regarding relations among lateralization of processes and lateralization patterns, following the four tested principles of lateralized processing. Blank fields imply that no specific prediction follows from the principle.

	Statistical Compl.	Causal Compl.	Input Asymmetry
functional segregation			
faces-words	no correlation	negative correlation	as low-level relation
global-local	no correlation	–	as high-level relation
LSF-HSF	no correlation	–	as high-level relation
co-lateralization			
faces-global-LSF	no correlation	–	positive correlation
words-local-HSF	no correlation	–	positive correlation
spatial attention	no correlation	–	–
subgroup differences			
RH-dominant	typical pattern	reversed pattern	as low-level pattern
left-handed	typical pattern	–	as low-level pattern
right-handed	typical pattern	typical pattern	as low-level pattern

consistent patterns of contralateral and ipsilateral specialization can be found for participants who differ in terms of which hemisphere is dominant for language. Previous studies indeed suggested that individuals with RH-dominance for language can show absent or reversed lateralization of other processes, such as face processing (Gerrits et al., 2019) and spatial attention (Cai et al., 2013).

Furthermore, we actively sought to include as many left-handed participants (generally known to be more variable with regard to their lateralization of language [Knecht et al., 2000]) as possible so as to obtain a participant sample that could be expected to be heterogeneous with regard to hemispheric dominance for language. This resulted in subgroups of right-handed, left-handed (for whom language dominance was unknown), and (left-handed) RH-dominant participants.

As such, the present study deviated from many earlier lateralization studies in that the gathering of lateralization indices of a multitude of within-domain processes and the aimed for heterogeneity of our sample allowed for a thorough evaluation of predictions following the three principles of lateralized processing (Table 1). The statistical complementarity principle predicts the absence of correlations between lateralization indices of different processes, and based on this principle there is no reason to assume lateralization patterns other than the ‘typical’ one to occur. If, to the contrary, the lateralization of the investigated processes is not independent, the causal complementarity principle predicts negative¹ correlations between processes governed by homologue areas (i.e., the stronger LH-lateralization for words, the stronger RH-lateralization for faces). Following this prediction, lateralization patterns should be reversed for individuals for whom language dominance is reversely lateralized to the RH. The causal complementarity principle does not allow any predictions regarding lateralization of processes that do not become lateralized to homologue areas. As processing of

global form and local features (Chechlacz, Mantini, Gillebert, & Humphreys, 2015) and LSFs and HSFs (Peyrin, Baci, Segebarth, & Marendaz, 2004) have both been proposed to recruit differing cortical areas, no predictions regarding correlations between lateralization of these processes can be made based on the causal complementarity principle. Furthermore, based on the causal complementarity principle we cannot make any predictions regarding processes that are lateralized to the same hemisphere (i.e., ipsilateral processes such as face and global feature processing). The input asymmetry principle fills this gap by predicting both the direction of correlations and the lateralization patterns of higher-level ipsilateral processes to simply mirror those of lower-level processes. In addition, the input asymmetry principle predicts positive correlations between ipsilateral processes within a processing hierarchy (e.g., the stronger LH-lateralization for local processing, the stronger LH-lateralization for word processing). Based on previous studies on the relation between spatial attention, language production, face processing, and vision more generally (Badzakova-Trajkov et al., 2016; Liu et al., 2009), lateralization of spatial attention is predicted to be statistically independent from that regarding other processing domains.

2. Methods

2.1. Participants

2.1.1. Participant recruitment

Right- and left-handed participants were recruited at the University of Groningen, while only left-handed participants were recruited at the University of Ghent, from an existing left-handed participant pool. Part of the participants in this Ghent participant pool had undergone fMRI scanning in a previous study, establishing their RH-dominance for language (Van der Haegen et al., 2011). The final sample was based on pragmatic considerations, testing as many participants as we could get. Participants in Groningen who had participated in a previous study using the same tasks (Brederoo et al., 2019) were excluded from participation in the current study, to prevent unwanted practice effects or familiarity with the stimuli to influence the results.

¹ We here adhere to the common calculation of lateralization indices (see Methods), resulting in values smaller than 0 for RH-lateralization, and larger than 0 for LH-lateralization. Consequently, correlations describing a positive relation in terms of lateralization strength between two processes lateralized to opposite hemispheres, will numerically become negative correlations.

2.1.2. Participant sample

In total, 122 (69 women and 53 men) were tested²; 99 at the University of Groningen and 23 at Ghent University. Mean age of the participants was 21.3 years (range 17–35 years). All participants were native speakers of Dutch, German, or English, and reported normal or corrected-to-normal vision. Participants were classified as right-handed when they had a positive score on the Flinders Handedness Questionnaire, and as left-handed when they had a negative score on this questionnaire (Nicholls, Thomas, Loetscher, & Grimshaw, 2013). Twenty-three people from the left-handed Ghent participant pool signed up to participate, of whom 13 had known RH-dominant for language as verified with a verbal fluency task during fMRI scanning (Van der Haegen et al., 2011). Accordingly, our participant sample could be grouped into right-handed participants ($n = 69$), left-handed participants of whom hemispheric dominance for language was unknown ($n = 40$, including the 10 Ghent participants who had not undergone fMRI scanning), and left-handed RH-dominant participants ($n = 13$).

Participants received course credit or a monetary compensation for their participation. The ethical committee of the Psychology Department of the University of Groningen approved the experimental procedure, and all participants gave informed consent before the start of the experiment.

2.2. Tasks

Over the past decades of lateralization research, a wide variety of tasks have been devised to measure lateralization of information processing. For the current study, we used a series of tasks that we have previously shown to produce reliable evidence for population-typical visual lateralization in right-handed participants (Brederoo et al., 2019). A detailed description of these tasks and their methods can thus be found in our earlier study. The only general difference to the earlier study is that in the present study an in-house manufactured button box was used to collect responses in all tasks. A short description of each of the tasks will now follow, and the minor differences to the earlier study (Brederoo et al., 2019) will be mentioned.

In the *face similarity task* (Brederoo et al., 2019) –assessing lateralized face processing–, participants were presented with a neutral face image and two symmetrical composites of that same image: one consisting of twice the left side, the other of twice the right side of the original image. Participants then had to judge which of the two composite faces resembled the original image most. In the *lexical decision task* (Hausmann et al., 2019; Willemin et al., 2016) –assessing lateralized word processing–, participants saw strings of letters to the left and right of a central fixation point. Participants had to indicate whether the left, right, or neither of the letter strings was a valid word. In the *picture matching task* (Peyrin, Mermillod, Chokron, & Marendaz, 2006) –assessing lateralized spatial frequency processing–, participants were presented with images of natural scenes. A first centrally presented image (S1)

was followed by the same or a different image (S2) to the left or right of central fixation, the latter one being filtered to contain only relatively low or high spatial frequencies. Participants indicated whether the S1 and S2 had depicted the same natural scene. Of note is the fact that in our previous replication study, the picture matching task produced less convincing results than the other tasks used in the current study (Brederoo et al., 2019). We opted to use it nevertheless, as we were unaware of a more suitable task to measure lateralization of spatial frequency processing. In the *hierarchical letter task* (Brederoo, Nieuwenstein, Lorist, & Cornelissen, 2017) –assessing lateralized global form and local feature processing–, participants were shown so-called Navon letters, one to the right and one to the left of a central fixation point. A pre-specified target letter could appear as the local elements making up one of the Navon letters, as the global Navon letter, or be absent. Participants indicated whether the target letter had been present. In contrast to the earlier study (Brederoo et al., 2019), only bilateral presentation was used and the presentation durations were slightly different: a trial started with a blank screen, lasting 280 msec, followed by a centrally displayed fixation asterisk for 500 msec, and the Navon letters were presented for 100 msec. In the *landmark task* (Cai et al., 2013; Linnell, Caparos, & Davidoff, 2014) –assessing spatial attention bias–, participants were presented with a horizontal line that was transected by a vertical line at $.2^\circ$, $.6^\circ$, or 1° to the left or right from the midpoint.³ Participants had to judge whether the transection occurred to the left or right of the midline.

2.3. General procedure

The experiments took place in a darkened and sound-attenuated room. Distance to the monitor (22", 1280 × 1024, 100 Hz in Groningen; 24", 1920 × 1080, 100 Hz in Ghent) was kept fixed using a chin rest to ensure stability of the visual angle. All experimental tasks were run in E-Prime (E-prime Psychology Software Tools Inc., Pittsburgh, USA), and were preceded by the Flinders Handedness Questionnaire to measure handedness and the Dolman Method to measure eye dominance. As eye dominance is not a focus of this study, we will not elaborate further on it.

As the strength of RH-lateralization in the landmark task has been suggested to decrease over the course of an experimental session (Manly, Dobler, Dodds, & George, 2005), participants always completed this task at the start of the session. After that, the participants performed the remaining tasks (face similarity; lexical decision; picture matching; and hierarchical letter tasks), the order of which was randomized and counter-balanced over participants.⁴

³ Due to a coding error, participants in Groningen additionally received trials with a transection at 1.4° to the right of the midpoint. These trials are not included in the analyses.

⁴ Eighty-six of the participants came back for a second session at the same time of day seven days after they had taken part in the first session. The inclusion of this second session is irrelevant to the purposes of the current study as it served to examine previous suggestions that lateralization effects may dissipate with repeated exposure to a certain task (Jager & Postma, 2003).

² One additional participant was tested in Groningen, but was suspected to be drunk. This participant's data are not included in any of the analyses.

2.4. Data pre-processing

Before analyses, we inspected the data per task to remove the data of participants who performed at chance level. To do so, error rates (ERs) were computed separately for left visual field (LVF) and right visual field (RVF) trials in the visual half-field tasks. A participant's data were removed only when he or she performed at chance level in both the LVF and RVF, assuming that when performance is at chance level in one but not the other visual field this could be considered to reflect lateralization rather than poor performance. Removing data when performance in both visual fields was at chance resulted in missing data of 1 participant for word processing, 1 for LSF processing, 1 for HSF processing, 10 for local processing, and 1 for global processing. Due to a coding error, 2 participants' data were lost for spatial attention.

We used the outlier removal procedure as described by [Van Selst and Jolicoeur \(1994\)](#) to remove outliers in the RT data. This resulted in the removal of 1.64% of the trials in the hierarchical letter task, 2.23% in the lexical decision task, and 2.58% in the picture matching task.

For each of the tasks, we first conducted analyses to confirm that they produced the expected, population-typical lateralization effects. LVF and RVF performance were compared using paired t-tests on ERs and RTs to assess lateralized processing of LSF and HSF, global and local, and word processing. Lateralization of face processing and spatial attention were assessed with a one-sample t-test, testing the difference of the visual field bias against zero.

The results of these analyses, reported in [Appendix A](#), showed that, except for the picture matching task, all of the tasks indeed produced the expected lateralization effects, thus corroborating the findings of our earlier study ([Brederoo et al., 2019](#)).

2.5. Correlation analysis

2.5.1. Outcome variables for correlational analyses

The main analysis of interest examined the correlations between lateralization indices of the different processes. To assess the degree of lateralization for each process, we derived a scaled index for the extent to which performance and judgments differed for stimuli shown in the left and right visual fields. For performance-based measures (i.e., error rates and reaction times), this index was computed by subtracting a participant's RVF-performance from his or her LVF-performance, and dividing it by the sum of both. Accordingly, positive values for these indices indicate the presence of an RVF-advantage, suggestive of LH-dominance for the task in question, whereas negative values indicate the presence of an LVF-advantage.

For the face similarity task, an analogue to a performance-based index of lateralization was derived by subtracting the proportion of choice for the right composite face (indicating that participants judged the face based on the facial information on the right side) from the proportion choice for the left composite face (indicating that participants judged the

face based on the facial information on the left side). Thus, negative values on this measure of the face similarity task indicate an LVF-advantage in processing faces, while positive values indicate an RVF-advantage.

Lastly, for the landmark task, the index of lateralization was defined as the point of subjective equality (PSE), with 0 being assigned to the veridical point of equality. Consequently, negative values for the outcome of the landmark task indicate an LVF-bias suggestive of RH-dominance in allocating spatial attention, whereas positive values indicate an RVF-bias indicative of LH-dominance in spatial attention.

2.5.2. Statistical analysis of correlations

To assess the extent to which our data supported the presence (H1) or absence (H0) of the hypothesized correlations (see section 1.1), we used Bayesian analyses. An advantage of Bayesian statistics over null hypothesis significance testing (NHST) is that it provides information about the likelihood of the null hypothesis being true, given the data. In contrast, NHST only allows for rejection of the null hypothesis. Specifically, in Bayesian analyses, evidence is based on the relative plausibility of the data under the alternative (H1) versus the null hypothesis (H0) ([Wagenmakers et al., 2017](#)). A Bayesian analysis produces a Bayes factor (BF_{10}), where $BF_{10} > 3$ indicates moderate, $BF_{10} > 10$ indicates strong, $BF_{10} > 30$ indicates very strong, and $BF_{10} > 100$ indicates extreme evidence for H1, while $BF_{10} < 1/3$ indicates moderate, $BF_{10} < 1/10$ indicates strong, $BF_{10} < 1/30$ indicates very strong, and $BF_{10} < 1/100$ indicates extreme evidence for H0 ([Jeffreys, 1961](#)). When the BF_{10} ranges between 3 and $1/3$, the data are said to be inconclusive with regard to the hypotheses. We computed pairwise correlations for each possible pair of lateralization effects using the `libDienesBayes` package in R, and used a uniform prior (making no specific predictions with regard to the strength of the correlations) with the lowest split-half reliability of the two correlated lateralization indices as upper bound. The reported correlations were corrected by accounting for the split-half reliabilities of both measures ($r_{corrected} = r / \sqrt{[reliability_1 * reliability_2]}$). These choices for an upper bound of the lowest split-half reliability in the Bayesian analyses, and for correction of the correlations with the split-half reliabilities, were made on the grounds that a measure cannot show a larger correlation with another measure than it can with itself. Split-half reliability was computed as the correlation between lateralization indices for odd and even trials in each task, corrected for halving the length of the task by means of the Spearman-Brown formula, and can be found in [Appendix A](#). In each of the tasks, there were equal numbers of LVF- and RVF-trials within blocks, and randomized presentation order per participant, warranting the calculation of split-half reliabilities.

2.6. Subgroup-comparisons

We contrasted the lateralization effects for right-, left-handed, and RH-dominant participants. All these paired contrasts were made using one-sided Bayesian t-tests, based on the associated hypotheses (see section 1.1).

3. Results

In all tasks, there was substantial evidence for the expected RVF- and LVF-advantages, with the exception of those in the picture matching task, which showed no evidence for the presence of an RVF-advantage for HSF processing (see [Appendix A](#)). Nevertheless, we did include this non-significant RVF-advantage in all following analyses, as there could still be a relation of HSF-lateralization to lateralization of the other processes and/or differences between subgroups. Split-half reliability of each of the measures was good (all $BF_{10} > 38$), ranging from $r = .45$ for HSF processing to $r = .86$ for word processing (see [Appendix A](#)).

In the following, for all derived laterality indices and statistics, positive values indicate RVF/LH-lateralization, and negative values indicate LVF/RH-lateralization.

3.1. Correlations between lateralization indices

We here report the correlations for which we found at least substantial evidence in favor of their presence (see [Fig. 1](#)) or absence. An overview of all correlations, including those for which the data were inconclusive, can be found in [Appendix A](#).

Lateralization of face processing related to lateralization of three other processes. The stronger RH-lateralization for face processing, the stronger (1) LH-lateralization for word processing (RTs)⁵ ($r_{corrected} = -.29$, $BF_{10} = 6.12$, $t[119] = -2.42$); (2) LH-lateralization for local processing (RTs) ($r_{corrected} = -.33$, $BF_{10} = 8.76$, $t[110] = -2.55$); and (3) RH-lateralization for global processing (ERs) ($r_{corrected} = .39$, $BF_{10} = 11.15$, $t[119] = 2.53$). There was no correlation between face lateralization and lateralization of HSF or LSF processing ($BFs < .303$).

Second, in addition to its relation with face processing, word processing also correlated with local processing: the stronger LH-lateralization for word processing (RTs), the stronger LH-lateralization for local processing (RTs) ($r_{corrected} = .30$, $BF_{10} = 6.49$, $t[109] = 2.47$). Stronger LH-lateralization for local processing (ERs) was in turn associated with stronger LH-lateralization for HSF processing ($r_{corrected} = .52$, $BF_{10} = 17.9$, $t[108] = 2.67$). In testing the associations between contralateral lateralization for lower-level processes we found that stronger RH-lateralization for global processing (ERs) was associated with stronger LH-lateralization for local processing (ERs) ($r_{corrected} = -.37$, $BF_{10} = 3.01$, $t[109] = -1.92$), but that stronger RH-lateralization for LSF processing was associated with weaker LH-lateralization for HSF processing ($r_{corrected} = .47$, $BF_{10} = 29.7$, $t[118] = 2.87$).

There were no relations between spatial attention bias and lateralization of the other visual processes, with inconclusive evidence with regard to positive relations with lateralization of global processing ($BF_{10} = .629$, $t[112] = .945$) and that of word

processing ($BF_{10} = .532$, $t[112] = 1.16$), and support for the absence of any relations with lateralization of the other processes (all $BF_{10} < .25$, $|t| < .529$).

3.2. Lateralization indices per subgroup

Lateralization indices per subgroup can be found in [Fig. 2](#). Right-handed participants as a group showed all typical lateralization effects ($BF_{10} > 4.9$, $|t| > 2.5$), except for inconclusive evidence with regard to LH-lateralization for HSF processing ($BF_{10} = .591$, $t[67] = 1.37$).

Left-handed participants showed typical lateralization effects ($BF_{10} > 12.76$, $|t| > 2.9$), except for the absence of RH-lateralization for LSF processing ($BF_{10} = .104$, $t[38] = .783$) and RH spatial attention bias ($BF_{10} = .266$, $t[38] = -.5$), and they showed inconclusive evidence with regard to RH-lateralization for face processing ($BF_{10} = 1.51$, $t[39] = -1.84$), and LH-lateralization for HSF processing ($BF_{10} = .389$, $t[38] = .862$).

RH-dominant participants did not show the expected reversed lateralization effects (all $BF_{10} < 2.37$ for reversed effects), but did not show typical lateralization either, as for all types of processing typical effects were absent or data were inconclusive. Specifically, in RH-dominant participants the evidence supported the absence of RH-lateralization for face processing ($BF_{10} = .193$, $t[12] = .571$), of RH-lateralization for LSF processing ($BF_{10} = .279$, $t[12] = -.005$), and of LH-lateralization for HSF processing ($BF_{10} = .163$, $t[12] = -.912$). Furthermore, LH-lateralization for word processing for RH-dominant participants was absent in RTs ($BF_{10} = .113$, $t[12] = -1.98$), and data were inconclusive regarding this effect in ERs ($BF_{10} = 1.44$, $t[12] = 1.61$). Similarly, LH-lateralization for local processing was absent in RTs ($BF_{10} = .161$, $t[11] = -1.03$), and data were inconclusive in ERs ($BF_{10} = .747$, $t[11] = 1.05$). With regard to RH-lateralization for global processing, data were inconclusive both in ERs ($BF_{10} = 1.13$, $t[11] = -1.4$) and RTs ($BF_{10} = .348$, $t[11] = -.247$).

In addition to lateralization indices, proportions of participants who show typical lateralization within a subgroup can be informative on the direction of lateralization for different processes. A table reporting these proportions can be found in [Appendix A](#).

3.2.1. Differences between subgroups

Group-wise comparisons between the three groups showed that right-handed participants had stronger RH-lateralization for face processing than left-handed participants ($BF_{10} = 5.43$, $t[82] = -2.42$) and than RH-dominant participants ($BF_{10} = 25.49$, $t[15] = -2.73$). Right-handed participants also had stronger LH-lateralization for word processing (RTs) than RH-dominant participants ($BF_{10} = 1445$, $t[16] = 4.24$). Finally, they had stronger RH-lateralization for LSF processing than left-handed participants ($BF_{10} = 8.38$, $t[103] = -2.92$).

RH-dominant participants, furthermore, differed from left-handed participants in weaker LH-lateralization for word processing (RTs) ($BF_{10} = 94.71$, $t[18] = 3.38$), and local processing (RTs) ($BF_{10} = 5.21$, $t[23] = 2.7$), and weaker RH-lateralization for global processing (RTs) ($BF_{10} = 6.15$, $t[15] = -2.06$).

In addition to the presence of these subgroup differences, we found support for the absence of a number of differences.

⁵ We deem ERs and RTs to be reflective of the same lateralized processing –lateralization effects in ERs and RTs of the same processes were always in same direction (see [Appendix A](#)) and did not correlate in an opposing manner with other lateralization effects–, and here report the highest of correlations in ERs and RTs, when lateralization of a process correlates substantially with lateralization of another in both these measures.

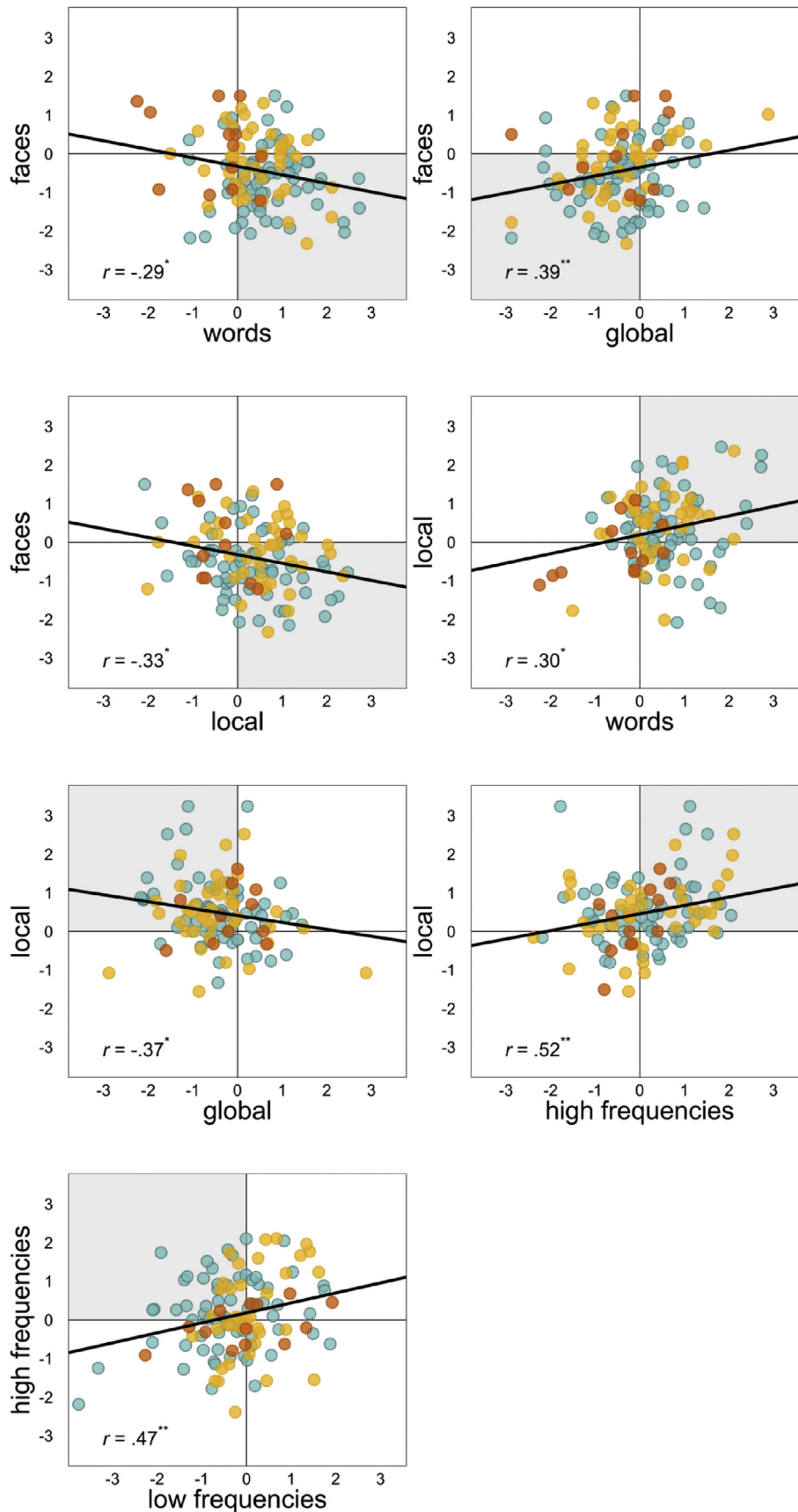


Fig. 1 – Correlations between scaled lateralization indices of right-handed (blue), left-handed (yellow), and RH-dominant (orange) participants. In each diagram, the grey-colored area depicts the locus of typical lateralization patterns. Larger positive and negative values indicate larger RVF- and LVF-advantages, respectively. ** $BF_{10} > 10$; * $BF_{10} > 3.16$.

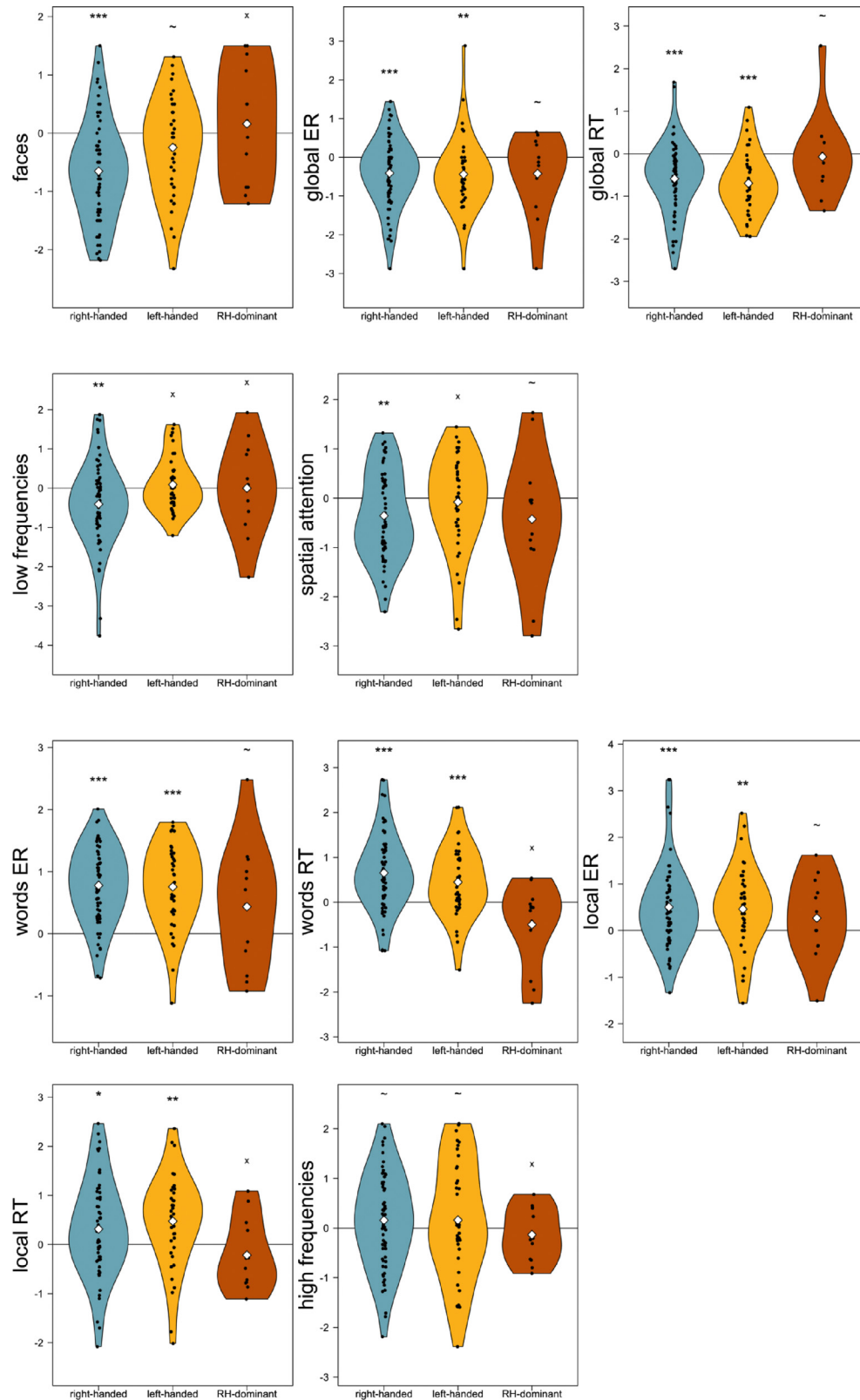


Fig. 2 – Lateralization indices and accompanying probability densities for right-handed, left-handed, and RH-dominant participants. Represented values are the scaled indices by dividing by the root mean square. White diamonds represent the means, where larger positive and negative values indicate larger RVF- and LVF-advantages, respectively. * $BF_{10} > 100$; ** $BF_{10} > 10$; * $BF_{10} > 3.16$; ~ $BF_{10} > .316 < 3.16$; x $BF_{10} < .316$, where H_1 is that the mean is higher or lower (depending on the hypothesis) than zero.**

Right-handed participants did not differ from left-handed participants with regard to lateralization of local processing in ERs ($BF_{10} = .258$, $t[85] = .234$) or RTs ($BF_{10} = .128$, $t[86] = -.831$), of global processing in ERs ($BF_{10} = .186$, $t[76] = .159$) or RTs ($BF_{10} = .134$, $t[92] = .717$), of word processing (ERs) ($BF_{10} = .243$, $t[77] = .184$), and in HSF processing ($BF_{10} = .209$, $t[67] = -.014$). Right-handed participants did not differ from RH-dominant participants with regard to lateralization of global processing (ERs) ($BF_{10} = .3$, $t[14] = .039$), or in spatial attention bias ($BF_{10} = .255$, $t[14] = .183$). RH-dominant participants did not differ from left-handed participants with regard to lateralization of LSF processing ($BF_{10} = .25$, $t[15] = .265$), or in spatial attention bias ($BF_{10} = .174$, $t[17] = .88$).

Evidence was inconclusive for all other pairwise comparisons between the subgroups ($BF_{10} > .33 < 2.57$, $|t| < 1.74$).

4. Discussion

4.1. Summary of results

Before evaluating our findings in light of the previously proposed principles underlying patterns of lateralization, we present a short summary of the results. As predicted, group-level analyses indeed gave rise to a ‘typical’ pattern of lateralization: left hemisphere (LH) processing of words and local features; right hemisphere (RH) processing of faces, global form, and low spatial frequencies (LSF), and a RH spatial-attention bias. The evidence for the expected LH-lateralization of high spatial frequency (HSF) information processing was not substantial, confirming neither its presence nor its absence in the group as a whole.

In addition to the group-level analyses, we investigated possible differences between right-handed, left-handed, and RH-dominant participants. We found that, as a group, right-handed participants showed the typical lateralization pattern, with the exception of LH-lateralization for HSF processing. RH-dominant participants did not show the expected reversed lateralization pattern, but their results were characterized by an absence of lateralization effects, with the exception of inconclusive data with regard to RH-lateralization for global processing and RH spatial attention bias. Left-handed participants showed results more similar to right-handed participants than did the RH-dominant participants, but still deviated from the typical pattern. For left-handed participants, RH-lateralization for LSF processing and RH spatial attention bias were absent, and the data were inconclusive with regard to RH-lateralization for face processing and LH-lateralization for HSF. Left-handed participants did show typical lateralization for word, local, and global processing.

4.2. Principles governing patterns of lateralized processing

When considering the implications of the current findings for the previously proposed principles underlying patterns of lateralization, we can conclude that the input asymmetry and causal complementarity principles are best supported (Table 2). These principles are not mutually exclusive, but rather

complement each other in explaining how lateralization of related processes comes about.

4.2.1. Mixed support for causal complementarity

In accordance with the causal complementarity principle (Bryden et al., 1983), which proposes that different processes recruiting similar brain regions will come to be lateralized to homologue areas in opposite hemispheres, our correlational analyses support a relation between LH-lateralization for word processing and RH-lateralization for face processing, where an increase of one co-occurs with an increase in the other. This is in line with a similar correlation found between the strength of LH-lateralization for visual word processing and that of RH-lateralization for face processing in a group of children who were learning to read (Dundas et al., 2015). Our results furthermore corroborate those reported by Badzakova-Trajkov et al. (2010) and Gerrits et al. (2019). In both these neuroimaging studies, LH-lateralization of brain regions activated during language production (i.e., letter fluency task) correlated with RH-lateralization of brain regions activated during face perception.

While the causal complementarity principle further predicts reversed lateralization patterns (i.e., LH-lateralization for face processing and RH-lateralization for word processing) for individuals who are RH-dominant for language, our data did not support such a pattern. Instead, the subgroup of participants who were RH-dominant for language showed an absence of RH-lateralization for face and LH-lateralization for word processing. One possible interpretation of the absence of reversed typical lateralization patterns in RH-dominant individuals is that causal complementarity is not a very strong driving force for functional segregation, resulting in subtle lateralization patterns. As a case in point, Badzakova-Trajkov et al. (2016) suggest that the mirroring of different functions to homologue areas does not take place as absolutely as the causal complementarity principle would dictate. Their results show that while –as predicted by the causal complementarity principle– one part of Broca’s homologue in the RH is activated by face stimuli (i.e., the pars opercularis), another part of Broca’s RH-homologue (i.e., the pars triangularis) is not. Relating to this, Häberling, Corballis, & Corballis (2016) entertain the possibility that lateralized brain systems can evolve following the causal complementarity principle (i.e., by competing pressure for cortical space), but once instantiated will go on to develop more independently. As a result, a directly observable relation between the functionally segregated functions will dissipate over the course of evolution.

Alternatively, it is possible that causal complementarity underlies the functional segregation of face and word processing, and that RH-dominant individuals in fact do tend to display reversed patterns, but that our sample of $n = 13$ was too small to detect this. What we can conclude based on our Bayesian analyses, is that in case of the RH-dominant participants the data supported the absence of typical lateralization of face and word processing. Due to practical limitations, we were unfortunately unable to enlarge our sample of RH-dominant participants.

Finally, these findings could indicate that lateralized processing in RH-dominant individuals does not adhere to the

Table 2 – Summary of results. ‘x’s appear where a prediction is not supported.

	Statistical Compl.	Causal Compl.	Input Asymmetry
functional segregation			
faces-words	x	negative correlation	as low-level relation
global-local	x	–	as high-level relation
LSF-HSF	x	–	x
co-lateralization			
faces-global-LSF	x	–	positive correlation
words-local-HSF	x	–	positive correlation
spatial attention	no correlation	–	–
subgroup differences			
RH-dominant	x	x	as low-level pattern
left-handed	x	–	as low-level pattern
right-handed	typical pattern	typical pattern	as low-level pattern

same principles as it does in LH-dominant individuals. Given the scarcity ($\pm 6\%$, [Knecht et al., 2000](#)) of RH-dominance for language, it is unsurprising that our understanding of lateralization in this group of individuals is limited as of yet (see also [Vingerhoets, 2019](#)). Our results can be taken as encouragement for future research to further explore lateralized processing in its atypical as well as typical form.

4.2.2. Support for input asymmetry

In support of the input asymmetry principle, we found the predicted correlations between lateralization of low-level processes and lateralization of associated higher-level processes in the same hemisphere ([Andresen & Marsolek, 2005](#)). The only such predicted relation for which we did not find conclusive support was that between lateralization of face and LSF processing. Specifically, as predicted by the input asymmetry principle, we generally found that stronger LH-lateralization for local feature processing was associated with stronger LH-lateralization for word- and HSF-processing. Complementing this, stronger RH-lateralization for face processing was associated with stronger RH-lateralization for global form processing. We further found that stronger RH-lateralization for face processing was associated with stronger LH-lateralization for local feature processing. However, the input asymmetry principle also predicted positive relations between RH-lateralization for face processing and LSF processing, and between LH-lateralization for word processing and HSF processing; relations which were absent in the present study. The input asymmetry principle further predicted the relation of lower-level processes to mirror those of higher-level processes. Indeed, in our data the stronger RH-lateralization for global processing was associated with stronger LH-lateralization for local processing, which is in accordance with the relation between the higher-level face and word processing.

Furthermore, rather than making predictions with regard to typical and atypical lateralization patterns in individuals varying in handedness and hemispheric dominance for language, the input asymmetry principle predicts that whatever is the pattern found for lower-level processes, should be the pattern found for higher-level processes. Indeed, our results support this notion in that (1) typical lateralization of spatial frequencies (with the exception of HSF processing) and global

and local processing co-occurred with typical lateralization of face and word processing; and (2) the absence of lateralization of spatial frequencies co-occurred with absence of lateralization of face and word processing in RH-dominant individuals. As such, lateralization patterns, or lack thereof, of higher-level processes mirrors that of lower-level processes.

4.2.3. Statistical complementarity for attention and vision

According to the statistical complementarity principle, the distribution of lateralization of different processes arises by chance ([Bryden et al., 1983](#)). Based on a factor analysis of neuroimaging data, [Liu et al. \(2009\)](#) suggested that such independent lateralization is the case for the domains of vision, language, attention, and internal thought. In line with [Liu et al. \(2009\)](#), we showed that spatial attention bias does not relate to lateralization of any of the other processes, and as such can be considered to be statistically independent from lateralization of the remaining visual processes under study. This is in line with the factor-analysis reported in [Badzakova-Trajkov et al. \(2016\)](#), which also suggested the existence of independently lateralized brain systems for face processing and spatial attention. Furthermore, in showing that our handedness groups differed in language lateralization but not in spatial attention bias, we corroborated earlier findings ([Badzakova-Trajkov et al., 2010](#); [Karlsson, Johnstone, & Carey, 2019](#)), and provided further support for statistical independence of spatial attention and language lateralization.

However, our results differ from two earlier studies showing support for causal complementarity of spatial attention and language production ([Cai et al., 2013](#); [Zago et al., 2015](#)). Specifically, these studies showed reversed typical patterns consisting of LH-lateralization for spatial attention and RH-lateralization for verbal fluency in a group of RH-dominant individuals ([Cai et al., 2013](#)), and a correlation between RH-lateralization for spatial attention and LH-lateralization for language production in a group of left-handed participants ([Zago et al., 2015](#)). In accommodating these differences with our results, it is important to note that our sample included right-handed as well as left-handed participants, while these results by [Cai et al. \(2013\)](#) and [Zago et al. \(2015\)](#) are based on groups consisting solely of left-handed participants. [Zago et al. \(2015\)](#) separately tested a group of right-handed participants, and found no evidence for

a relation between spatial attention and language within this group. In the study by Zago et al. (2015), right-handed and left-handed participants were not pooled together for the analyses, unfortunately precluding a direct comparison with our results. In relation to this, Gerrits et al. (2019) –using a sample of only left-handed participants, failed to show a relation between lateralization for face processing and visual word processing (with $p = .065$), while in our data this correlation was evident. These observations may be taken as a reminder of caution in selecting participants; while in laterality research it is important and fortunately good custom to include left-handed participants, the exclusion of right-handed participants may come with its own price. To prevent the emergence of incomplete or distorted depictions of lateralization patterns, future research on this topic should use participant samples that are maximally heterogeneous with regard to handedness and hemispheric dominance for language.

Finally, we showed that lateralization of processes within the domain of vision are not statistically independent: lateralization of each of the measures of visual information processing was correlated to lateralization of another. Furthermore, the statistical complementarity principle predicts there to be no difference in lateralization patterns between individuals based on their handedness and/or hemispheric dominance for language. As described above, right-handed, left-handed, and RH-dominant participants were in fact shown to differ in terms of lateralization patterns, further discrediting the notion of independent lateralization of the visual processes under study. Taken together, our results support statistical independence of the lateralization of attention and vision, but not within the domain of vision.

4.3. Conclusion

In sum, the typical and deviating patterns of lateralization of face, word, global form, local feature, low and high spatial frequency processing can best be explained by the governing principles of input asymmetry and, to a lesser extent, causal complementarity. Our results are partly in line with the notion that processes recruiting similar resources will come to be lateralized to homologue areas in a manner that promotes intra-hemispheric proximity to other cortical areas within their processing hierarchies. In the case of word and face processing, the former will be driven to the LH because of its specialization in language, local feature and high spatial frequency processing, while the latter will be driven to the RH because of its specialization in global form and low spatial frequency processing. We further suggest that statistical complementarity applies to the relation between lateralization of attention and vision.

In the present study, group-level analyses gave rise to typical lateralization patterns, while separate analyses for subgroups differing in terms of handedness and RH-dominance for language provided a more nuanced view. Future research should keep studying lateralized processing in individuals who are expected to deviate from typical patterns, so as to increase our understanding of hemispheric specialization in all its diversity and complexity.

Credit author statement

Sanne G. Brederoo: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft. Lise van der Haegen: Investigation, Writing – Review & Editing. Marc Brysbaert: Conceptualization, Writing – Review & Editing, Supervision. Mark N. Nieuwenstein: Conceptualization, Writing – Review & Editing, Supervision. Frans W. Cornelissen: Writing – Review & Editing, Supervision. Monique M. Lorist: Writing – Review & Editing, Supervision.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Data and analysis scripts are publicly available at <https://doi.org/10.17605/OSF.IO/QYMFB> (Open Science Framework). This is stated on page 12 of the manuscript.

Declaration of competing interest

None.

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedures or analyses was pre-registered prior to the research being conducted. Analysis scripts, data, and experiment programs can be accessed at <https://doi.org/10.17605/OSF.IO/QYMFB>.

Acknowledgements

S.G. Brederoo was supported by a PhD scholarship as part of grant 022.004.008 awarded to the Research School for Behavioural and Cognitive Neuroscience (BCN) by the Netherlands Organisation for Scientific Research (NWO). We thank Heike Schuler, Louisa La Porta, Lukas Kowald, and Soma Makai-Boloni for their assistance in data collection. We are grateful to Michael Corballis and David Carey for their helpful comments on a previous draft of this manuscript.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2020.08.029>.

REFERENCES

- Andresen, D. R., & Marsolek, C. J. (2005). Does a causal relation exist between the functional hemispheric asymmetries of visual processing subsystems? *Brain and Cognition*, 59(2), 135–144. <https://doi.org/10.1016/j.bandc.2005.05.010>

- Badzakova-Trajkov, G., Corballis, M. C., & Häberling, I. S. (2016). Complementarity or independence of hemispheric specializations? A brief review. *Neuropsychologia*, 93, 386–393. <https://doi.org/10.1016/j.neuropsychologia.2015.12.018>
- Badzakova-Trajkov, G., Häberling, I. S., Roberts, R. P., & Corballis, M. C. (2010). Cerebral asymmetries: Complementary and independent processes. *Plos One*, 5, Article e9682. <https://doi.org/10.1371/journal.pone.0009682>
- Behrmann, M., & Plaut, D. C. (2013). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in Cognitive Sciences*, 17, 210–219.
- Behrmann, M., & Plaut, D. C. (2015). A vision of graded hemispheric specialization. *Annals of the New York Academy of Sciences*, 1359, 30–46. <https://doi.org/10.1111/nyas.12833>
- Brederoo, S. G., Nieuwenstein, M. R., Cornelissen, F. W., & Lorist, M. M. (2019). Reproducibility of visual-field asymmetries: Nine replication studies investigating lateralization of visual information processing. *Cortex*, 111, 100–126.
- Brederoo, S. G., Nieuwenstein, M. R., Lorist, M. M., & Cornelissen, F. W. (2017). Hemispheric specialization for global and local processing: A direct comparison of linguistic and non-linguistic stimuli. *Brain and Cognition*, 119, 10–16.
- Bryden, M. P., Hécaen, H., & DeAgostini, M. (1983). Patterns of cerebral organization. *Brain and Language*, 20, 249–262. [https://doi.org/10.1016/0093-934X\(83\)90044-5](https://doi.org/10.1016/0093-934X(83)90044-5)
- Cai, Q., Van der Haegen, L., & Brysbaert, M. (2013). Complementary hemispheric specialization for language production and visuospatial attention. *Proceedings of the National Academy of Sciences of the United States of America*, 110, E322–E330.
- Chechlacz, M., Mantini, D., Gillebert, C. R., & Humphreys, G. W. (2015). Asymmetrical white matter networks for attending to global versus local features. *Cortex*, 72, 54–64.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2015). Variable left-hemisphere language and orthographic lateralization reduces right-hemisphere face lateralization. *Journal of Cognitive Neuroscience*, 27(5), 913–925. <https://doi.org/10.1162/jocn.2015.1162/jocn>
- Gerrits, R., Van der Haegen, L., Brysbaert, M., & Vingerhoets, G. (2019). Laterality for recognizing written words and faces in the fusiform gyrus covaries with language dominance. *Cortex*, 117, 196–204.
- Goffaux, V., & Rossion, B. (2006). Faces are “spatial” - holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology. Human Perception and Performance*, 32(4), 1023–1039. <https://doi.org/10.1037/0096-1523.32.4.1023>
- Häberling, I. S., Corballis, P. M., & Corballis, M. C. (2016). Language, gesture, and handedness: Evidence for independent lateralized networks. *Cortex*, 82, 72–85.
- Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Eccentricity bias as an organizing principle for human high-order object areas. *Neuron*, 34, 479–490.
- Hausmann, M., Brysbaert, M., Van der Haegen, L., Lewald, J., Specht, K., Hirnstein, M., et al. (2019). Language lateralisation measured across linguistic and national boundaries. *Cortex*, 111, 134–147.
- Hellige, J. B. (1993). *Perspectives in cognitive neuroscience. Hemispheric asymmetries: What's right and what's left*. Cambridge, MA: Harvard University Press.
- Ivry, R. B., & Robertson, L. C. (1998). *The two sides of perception*. Cambridge, MA: MIT Press.
- Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: A review of the current evidence. *Neuropsychologia*, 41, 504–515.
- Jeffreys, H. (1961). *Theory of probability* (3rd ed.). London: Oxford University Press.
- Karlsson, E. M., Johnstone, L. T., & Carey, D. P. (2019). The depth and breadth of multiple perceptual asymmetries in right handers and non-right handers. *Laterality: Asymmetries of Body, Brain and Cognition*, 24, 707–739.
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., et al. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123, 2512–2518.
- Linnell, K. J., Caparos, S., & Davidoff, J. (2014). Urbanization increases left-bias in line-bisection: An expression of elevated levels of intrinsic alertness? *Frontiers in Psychology*, 5, 1–7. <https://doi.org/10.3389/fpsyg.2014.01127>
- Liu, H., Stufflebeam, S. M., Sepulcre, J., Hedden, T., & Buckner, R. L. (2009). Evidence from intrinsic activity that asymmetry of the human brain is controlled by multiple factors. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 20499–20503.
- Manly, T., Dobler, V. B., Dodds, C. M., & George, M. A. (2005). Rightward shift in spatial awareness with declining alertness. *Neuropsychologia*, 43, 1721–1728.
- Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Percey, G., et al. (2014). Gaussian mixture modeling of hemispheric lateralization for language in a large sample of healthy individuals balanced for handedness. *Plos One*, 9, 9–14.
- Nicholls, M. E. R., Thomas, N. A., Loetscher, T., & Grimshaw, G. M. (2013). The Flinders handedness survey (FLANDERS): A brief measure of skilled hand preference. *Cortex*, 49, 2914–2926.
- Ossowski, A., & Behrmann, M. (2015). Left hemisphere specialization for word reading potentially causes, rather than results from, a left lateralized bias for high spatial frequency visual information. *Cortex*, 72, 27–39. <https://doi.org/10.1016/j.cortex.2014.12.013>
- Peyrin, C., Baci, M., Segebarth, C., & Marendaz, C. (2004). Cerebral regions and hemispheric specialization for processing spatial frequencies during natural scene recognition. An event-related fMRI study. *Neuroimage*, 23, 698–707.
- Peyrin, C., Mermillod, M., Chokron, S., & Marendaz, C. (2006). Effect of temporal constraints on hemispheric asymmetries during spatial frequency processing. *Brain and Cognition*, 62(3), 214–220. <https://doi.org/10.1016/j.bandc.2006.05.005>
- Rasmussen, T., & Milner, B. (1977). The role of early left-brain injury in determining lateralization of cerebral speech functions. *Annals of the New York Academy of Sciences*, 299, 355–369.
- Van Selst, M., & Jolicoeur, P. (1994). A solution to the effect of sample size on outlier elimination. *The Quarterly Journal of Experimental Psychology Section A*, 47, 631–650.
- Van der Haegen, L., & Brysbaert, M. (2018). The relationship between behavioral language laterality, face laterality and language performance in left-handers. *Plos One*, 13, 1–22.
- Van der Haegen, L., Cai, Q., Seurinck, R., & Brysbaert, M. (2011). Further fMRI validation of the visual half field technique as an indicator of language laterality: A large-group analysis. *Neuropsychologia*, 49(10), 2879–2888. <https://doi.org/10.1016/j.neuropsychologia.2011.06.014>
- Vingerhoets, G. (2019). Phenotypes in hemispheric functional segregation? Perspectives and challenges. *Physics of Life Reviews*, 10, 1–18.
- Wagenmakers, E.-J., Verhagen, J., Ly, A., Matzke, D., Steingrover, H., Rouder, J. N., et al. (2017). The need for Bayesian hypothesis testing in psychological science. In S. O. Lilienfeld, & I. D. Waldman (Eds.), *Psychological science under scrutiny: Recent Challenges and proposed solutions* (pp. 123–138). Chichester, UK: John Wiley & Sons Inc.
- Willemijn, J., Hausmann, M., Brysbaert, M., Dael, N., Chmetz, F., Fioravera, A., et al. (2016). Stability of right visual field advantage in an international lateralized lexical decision task irrespective of participants' sex, handedness or

- bilingualism. *Laterality: Asymmetries of body. Brain and Cognition*, 21, 502–524.
- Woodhead, Z. V. J., Wise, R. J. S., Sereno, M., & Leech, R. (2011). Dissociation of sensitivity to spatial frequency in word and face preferential areas of the fusiform gyrus. *Cerebral Cortex*, 21, 2307–2312. <https://doi.org/10.1093/cercor/bhr008>
- Zago, L., Petit, L., Mellet, E., Jobard, G., Crivello, F., Joliot, M., et al. (2015). The association between hemispheric specialization for language production and for spatial attention depends on left-hand preference strength. *Neuropsychologia*, 93, 349–406.